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记陕西蓝田晚中新世灞河组4种跳鼠(Dipodidae, Rodentia)化石[1)]

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摘要: 描述了陕西蓝田晚中新世早期灞河组的4属4种跳鼠:蓝田原跳鼠(新种)(*Protalactaga lantianensis* sp. nov.)、副跳鼠(未定种)(*Paralactaga* sp.)、原始三趾心颅跳鼠(新种)(*Salpingotus primitivus* sp. nov.)和小五趾心颅跳鼠(新种)(*Cardiocranius pusillus* sp. nov.)。蓝田原跳鼠兼有原跳鼠和副跳鼠的特征,可能是原跳鼠向副跳鼠进化过程中产生的一种过渡类型。副跳鼠和原始三趾心颅跳鼠及小五趾心颅跳鼠分别代表了副跳鼠属在中国的最早记录和心颅跳鼠亚科(Cardiocraniinae)在地史上的首次出现。4种跳鼠指示了蓝田地区当时的自然环境可能比现代更加干旱。

关键词: 陕西蓝田,晚中新世,灞河组,跳鼠科

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1 前言

现生的各种跳鼠广泛栖息于古北界的荒漠、荒漠草原及草原地区,从北非、西亚向东一直到中国北部与蒙古国的广大地区均有分布,为古北界所特有。跳鼠类高阶元的分类目前尚无一致意见,但古生物学者一般将跳鼠类动物分为林跳鼠科(Zapodidae)和跳鼠科(Dipodidae),后者又可分为4个亚科:五趾跳鼠亚科(Allactaginae)、三趾跳鼠亚科(Dipodinae)、心颅跳鼠亚科(Cardiocraniinae)和长耳跳鼠亚科(Euchoreutinae)(Daxner-Höck, 1999)。跳鼠科很可能是由近似于 *Plesiosminthus asiae-centalis* 一类的林跳鼠进化而来(邱铸鼎,1996),其最早的化石记录是中国甘肃泉头沟和内蒙古通古尔中中新世的 *Protalactaga* 属(Young, 1927;邱铸鼎,1996、2000)。中国现生的跳鼠科含有7属13种,分属上述4亚科,主要分布于西北地区的干旱地带(王应祥,2003)。

除中中新世的 *Protalactaga* 属外,中国的跳鼠科化石还有发现于华北和西北晚中新世以来的 *Paralactaga*、*Brachyscirtetes*、*Dipus* 和 *Alactaga* 属(Schlosser, 1924; Young, 1927; Boul and Teilhard, 1928; Teihard and Young, 1931; 郑绍华, 1982; Fahlbusch et al., 1983; Flynn et al., 1991; 邱铸鼎、王晓鸣, 1999; Qiu and Storch, 2000; 李强等,2003; Qiu, 2003; 李强、邱铸鼎,2005)。

本文记述的跳鼠科材料系中芬地层古生物工作者在执行“中国晚新生代数据库”合

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作项目时，于1997至2000年的4次野外工作中，在陕西蓝田晚中新世早期灞河组中采集到的。有关化石地点的地层概况和所发现的哺乳动物化石已有过初步报道（张兆群等，1999，2002；Qiu et al.，2003），其中鼠科、沙鼠科和牛科的部分材料已作了详细的分类描述（邱铸鼎等，2004a，b；陈冠芳、张兆群，2004）。

下述牙齿构造术语，引自Shenbrot（1984），略作补充修改。测量值表达式为最大长×最大宽，精确到0.1 mm。文中缩写：IVPP V 中国科学院古脊椎动物与古人类研究所脊椎动物化石编号；IZ 中国科学院动物研究所现生动物标本编号。

2 标本记述

跳鼠科 Dipodidae Fischer von Waldheim，1817

五趾跳鼠亚科 Allactaginae Vinogradov，1925

原跳鼠属 *Protalactaga* Young，1927

蓝田原跳鼠（新种）*Protalactaga lantianensis* sp. nov.

（图1）

1999 *Protalactaga* sp.，张兆群等，p.58，table 1

2002 *Protalactaga major*，张兆群等，p.170，table 1

2003 *Protalactaga major*，Qiu et al.，p.445，table 1

名称来源 Lantian，蓝田县的汉语拼音。

正型标本 左M1（2.49 mm×2.15 mm），IVPP V 14435。

模式产地 陕西蓝田第12地点。

副型标本 第12地点：44枚单个的牙齿（5P4；6M1；8M2；4M3；7m1；9m2；5m3），IVPP V 14436.1～44；第19地点：2枚单个的牙齿（2 M2），V 14436.45～46；第6地点：1右m2前部，V 14436.47；Ms 14地点：1右m2，V 14436.48。

测量 见表1。

表1 蓝田原跳鼠（新种）牙齿测量

Table 1 Tooth measurements of *Protalactaga lantianensis* sp. nov. (mm)

Tooth	Loc.	N	Length		Width	
			Mean	Range	Mean	Range
P4	12	5	0.92	0.87～0.99	0.93	0.90～1.00
M1	12	6	2.47	2.38～2.53	2.02	1.89～2.15
M2	12	7	2.19	2.10～2.30	1.86	1.70～1.97
	19	2	2.105	2.10～2.11	1.57	1.45～1.69
M3	12	4	1.405	1.37～1.45	1.39	1.35～1.45
m1	12	6	2.47	2.40～2.60	1.735	1.66～1.80
m2	12	7	2.37	2.25～2.55	1.78	1.71～1.90
	Ms 14	1	2.30		1.78	
m3	12	4	1.91	1.80～2.00	1.59	1.52～1.67

种征　较大型。齿尖丘脊形。M1～2 的原脊后内向靠近中脊，后脊显著后位，后边脊短而明显向后外倾斜。m1～2 的下次脊明显前外向靠近下中脊。第三臼齿相对退化。

描述　P4：冠面椭圆形，由一 C 字形脊和一外谷构成。单根，粗壮。

M1：冠面近矩形。舌侧主尖(原尖和次尖)比唇侧主尖(前尖和后尖)强壮。前边小尖与前边尖小，近等大。前尖与后尖大小相当，皆为丘形。中尖不明显。在 6 件完整的标本中，次小尖都很发达，其与次尖之间的凹陷很深。前边脊横向或略前外向倾斜。内脊前部微弯，后部强壮。原脊短，7 件标本中有 5 件指向后内，并与中脊基部连接，另 2 件则较横向地与内脊前部连接；中脊相对较粗，伸达齿缘，横向或略后外向。后脊后指与次小尖相连；后边脊粗短，向后外倾斜，未达外齿缘。4 牙根。

M2：基本形态与 M1 相似，只是后部较收缩；次尖、后尖和后边脊相对较弱；前尖和后尖相对更显前后压扁。原脊大多(8/10)较横向或后内向与内脊前部相连，另 2 枚深磨蚀的牙齿则与中脊中部连接。中脊只一枚牙齿朝后强烈弯曲并与后尖前壁接触。后脊只 2 枚牙齿明显横向并与次尖和后边脊的联合部连接。后边脊粗短，向后外倾斜，未达外齿缘。内谷更为前外向伸展。4 牙根。

M3：冠面呈圆三角形，前宽后窄。原脊与原尖前方连接。次尖和后尖相当退化，并与后边脊融合成一环绕后外部的脊，仅有 1 枚牙齿的后尖较独立。4 枚 M3 中，1 枚的中脊完全消失(图 1.13)；1 枚极弱(图 1.14)；2 枚发达且伸达齿缘。在后一种情形中，1 枚的中脊与后边脊之间形成小的坑(图 1.15)，另 1 枚的中脊与前尖由一纵脊连接，与后边脊之间的坑较大(图 1.16)。

m1：前窄后宽。下前边尖仅见于 1 枚牙齿，位于下后尖的前壁，小而位低(图 1.19)。唇、舌侧主尖交错排列，唇侧主尖相对后位。下原尖前外后内向伸展。6 枚完整的牙齿中，4 枚磨蚀程度较轻的下后尖近圆形，孤立于下原尖和下中脊；1 枚与下原尖连接；1 枚则与下中脊在近内齿缘处融合。下外中脊发达、粗短而呈三角形。下中脊较粗壮，强烈斜向前内侧，末端明显膨大。下次脊前外向与下原尖和下中脊的联合部连接。下外脊弯曲，在 3 枚磨蚀浅的牙齿中有小的间断。下次小尖发达，与下次尖之间的凹陷清晰，后边脊强壮。2 牙根。

m2：冠面近矩形。唇、舌侧主尖亦交错排列。下前边脊在 10 枚牙齿中半数不发育，3 枚极弱，只 2 枚较发达。下前边尖较明显，多与下原尖分离，只 3 枚牙齿有脊相连；均与下后尖融合并前唇后舌向磨蚀。下中脊斜向前内，但比 m1 的相对细弱。无下外中脊。10 枚牙齿中的 6 枚下外谷边缘发育有一小的附尖。下次脊前外向与下中尖基部连接。下内谷(下内尖与下中脊之间)比 m1 的明显狭窄。下外脊前部粗壮，后部细弱，2 枚磨蚀浅的牙齿有小的间断。下后边脊粗壮。

m3：冠面近长三角形，后部明显退化。下前边尖与下后尖融合，下原尖前方由一粗短的脊与其中部连接，下原谷明显。下中脊不发育或与下次尖和下后边脊融合，下内尖不发育。下后边谷(下内尖与下后边脊之间)在 3 枚牙齿上发育，为一个小坑或一极轻微的凹陷。下中谷(下后尖与下中脊间)同 m2 一样发达，下外谷深，较开阔。

比较与讨论　蓝田标本的形态具有原跳鼠属 *Protalactaga* 的特征，即：个体相对较小；颊齿低冠；丘脊形齿；M1～2 前边脊和前边尖发育弱，原脊在绝大多数标本上未直接与中

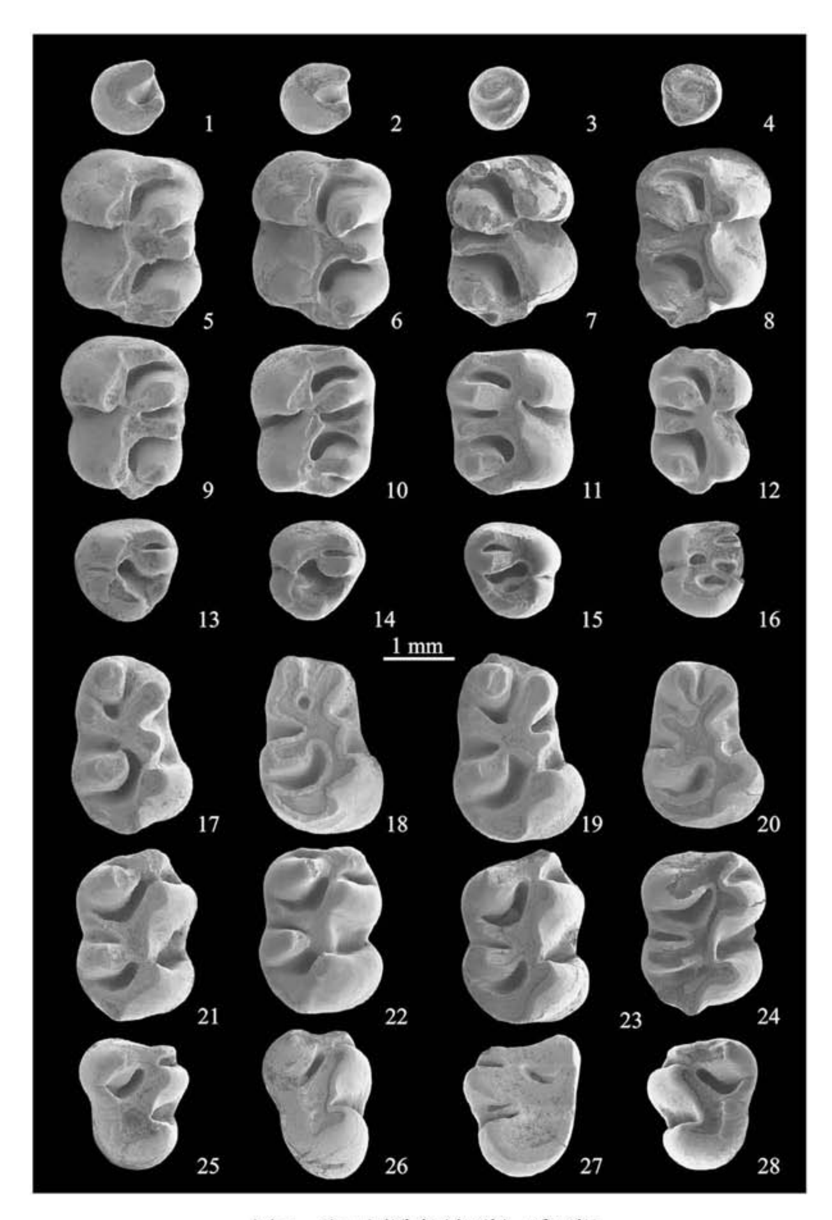


图1 蓝田原跳鼠(新种),嚼面视

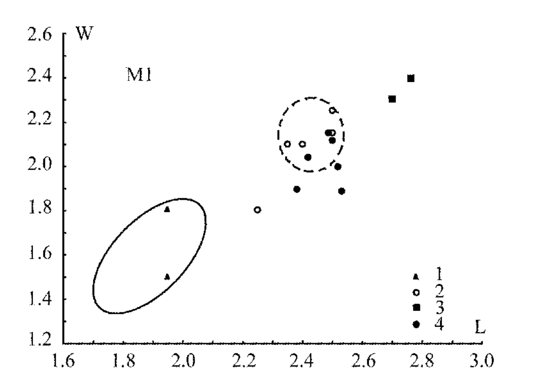
Fig. 1 *Protalactaga lantianensis* sp. nov., occlusal view

1. lP4 (V 14436.1); 2. lP4 (V 14436.2); 3. rP4 (V 14436.4); 4. rP4 (V 14436.5); 5. lM1, Holotype (V 14435); 6. lM1 (V 14436.10); 7. rM1 (V 14436.7); 8. rM1 (V 14436.9);9. l M2 (V 14436.14); 10. l M2 (V 14436.15); 11. rM2 (V 14436.13); 12. rM2 (V 14436.46); 13. lM3 (V 14436.21); 14. lM3 (V 14436.23); 15. rM3 (V 14436.20); 16. lM3 (V 14436.22);17. rm1 (V 14436.25); 18. rm1 (V 14436.27); 19. rm1 (V 14436.29); 20. rm1 (V 14436.28);21. rm2 (V 14436.35); 22. rm2 (V 14436.48); 23. rm2 (V 14436.36); 24. rm2 (V 14436.38); 25. rm3 (V 14436.42); 26. rm3 (V 14436.43); 27. lm3 (V 14436.40); 28. lm3 (V 14436.41)

脊连接;m1 具发达的下外中脊,m1 ~2 的下次脊未直接与下中脊连接。

Protalactaga 属迄今可以确定的有 3 种,即发现于中国甘肃泉头沟咸水河组和内蒙古通古尔组的模式种 *P. grabaui* 和 *P. major* (Young, 1927; Qiu, 1996, 2000)以及北非摩洛哥耶比雷的 *P. moghrebiensis* (Jaeger, 1977)。它们的时代均为中新世中期。发现于哈萨克斯坦渐新世晚期的 *P.* ? *borissiaki* 的材料仅为一带 M1 ~2 的上颌残段,其牙齿明显脊形,齿脊斜交于牙纵轴,中脊极不发育等(Argyropulo, 1939),显然不应归入 *Protalactaga* 属。

在牙齿的尺寸上,蓝田标本明显大于 *P. grabaui*, 但与 *P. major* 和 *P. moghrebiensis* 非常接近(见图 2)。形态上,蓝田标本以其 M1 ~2 的原脊、后脊指向明显偏后内;分别接近与中脊和后边脊直接连接,后边脊明显缩短和向后外倾斜;m1 ~2 的下次脊指向偏前外侧,与下中脊直接相连等特征明显区别于已知的三种原跳鼠。此外,蓝田标本与 *P. grabaui* 的不同还在于臼齿的齿脊更强壮,P4 的主尖不孤立,m1 的下前边尖几乎不发育,M3 中脊和 m3 下中脊极不发育甚至完全消失,使齿谷数相应减少等特征。与 *P. major* 的不同还在于其臼齿齿尖不像后者那样压扁,m1 的下前边尖几乎不发育,M3 和 m3 同样显得较退化等特征。与 *P. moghrebiensis* 的不同还在于其臼齿齿脊相对更强壮,m1 的下外脊更粗短。因此,蓝田标本应代表原跳鼠属中的一新种。



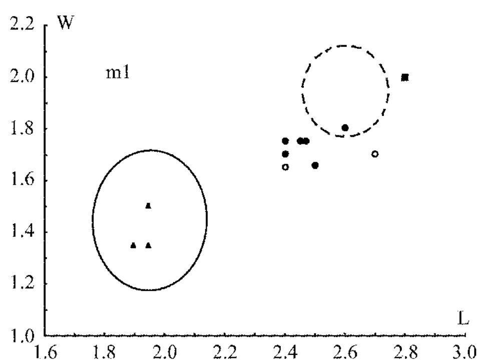


图 2　原跳鼠属各种第一臼齿测量数据散点图

Fig. 2　Scatter diagram showing length and width of the first molars of *Protalactaga*
Real line-*Protalactaga grabaui* (Quantougou); Broken line-*P. moghrebiensis* (Patanik 6, Maroc); 1. *P. grabaui* (Tunggur); 2. *P. major* (Quantougou); 3. *P. major* (Tunggur); 4. *P. lantianensis* sp. nov. (Lantian)

上述区别特征中最值得注意的是 M1 ~2 原脊和后脊以及 m1 ~2 下次脊连接方式的差异情况。在 *P. grabaui* 中,其 M1 的原脊绝大多数是较横向地与内脊连接,而 M2 的原脊几乎都是横向与原尖直接连接;在 *P. major* 和 *P. moghrebiensis* 中,M1 的原脊稍微内后向与内脊连接,M2 的原脊是较横向与内脊连接;而在 *P. lantianensis* 中,M1 的原脊明显内后向与内脊或中脊基部连接,M2 的原脊是明显内后向与中脊基部或中部连接。后脊在已知的三种原跳鼠的 M1 ~2 中都较横向地直接与次尖或稍微内后向与次小尖连接;而在 *P.*

lantianensis 中,后脊明显内后向与次小尖或后边脊连接。在 *P. grabaui*、*P. moghrebiensis* 和 *P. major* 中,m1 ~2 的下次脊都未与下中脊直接连接,下次脊在 m2 中相对于 m1 其指向更为横向,且与下中脊分得更开;而在蓝田原跳鼠(新种)中,m1 ~2 的下次脊都直接与下中脊基部直接连接。*P. lantianensis* 的 M1 ~2 的原脊和后脊以及 m1 ~2 的下次脊的连接方式与副跳鼠属 *Paralactaga* 较接近,但 *Paralactaga* 的 M1 ~2 的原脊和后脊分别向后与下中脊中部和后边脊连接,m1 ~2 的下次脊向前与下中脊中部连接。

新种部分第三臼齿的中脊和下中脊消失,齿谷数目相应减少,这一点明显不同于 *P. grabaui* 和 *P. major*, 而相似于 *P. moghrebiensis* 和 *Paralactaga*。*Protalactaga lantianensis* 所具有的与 *Paralactaga* 相似的齿脊的连接方式和简单退化的第三臼齿应是原跳鼠的衍生性状。这表明 *P. lantianensis* 似乎是正处于 *Protalactaga* 向 *Paralactaga* 进化过程中的一个过渡类型,代表了原跳鼠属的一进步种。

值得注意的是,无论牙齿的大小还是构造形态 *Protalactaga lantianensis* 都与副跳鼠属中的最小种,即甘肃天祝 80007 地点的"*Paralactaga minor*"(郑绍华,1982)高度相似。它们之间惟一的差别在于后者的那枚 m2 (V 6304)的下次脊直接与下中脊近中部连接,这一点和 *Paralactaga* 相似,但由于"*P. minor*"的材料太少,其齿脊指向和连接方式的变异情况尚不可知。若仅从个体小、低冠、尖脊发育相对弱等特征考虑,将"*P. minor*"归入 *Protalactaga* 属似乎更好,其类似于 *Paralactaga* 的尖、脊指向和连接方式可以同 *Protalactaga lantianensis* 一样解释为 *Protalactaga* 的进步性状。当然,"*P. minor*"确切的归属以及是否与 *Protalactaga lantianensis* 为同一种,还有待以后更多材料的发现。

副跳鼠属 *Paralactaga* Young, 1927

副跳鼠(未定种) *Paralactaga* sp.

(图3.1)

2002 *Paralactaga* sp. , 张兆群等, p. 170, table 1

2003 *Paralactaga* sp. , Qiu et al. , p. 445, table 1

材料 产自陕西蓝田 Ms 36 地点的一枚左 M3 (1.65 mm ×1.80 mm), IVPP V 14437。

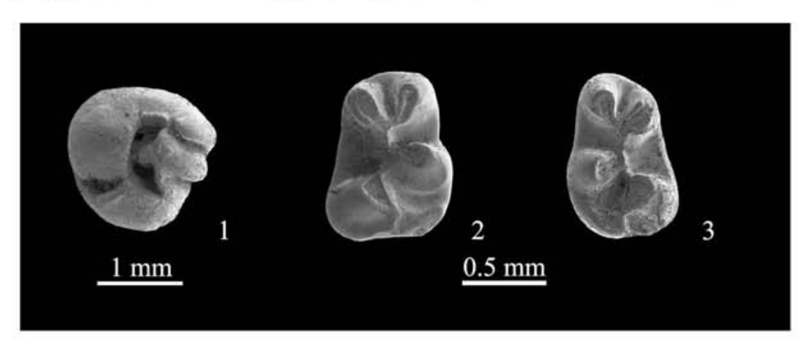


图3 1. 副跳鼠(未定种);2. 原始三趾心颅跳鼠(新种);3. 小五趾心颅跳鼠(新种),嚼面视

Fig. 3 1. *Paralactaga* sp. , lM3 (V 14437); 2. *Salpingotus primitivus* sp. nov. , lm1, Holotype (V 14438); 3. *Cardiocranius pussilus* sp. nov. , rm1, Holotype (V 14439), occlusal view

描述　冠面近三角形，未磨蚀。原尖显著膨大，前尖显著，前边尖明显。牙齿后部收缩，次尖退化，后尖小但明显。无中脊。前尖前方与前边脊中部连接，横向通过低而弱的原脊与原尖中部连接，后方有一小纵脊与后尖相连，使牙齿中间形成一封闭的新月型凹。牙齿唇侧前边附尖之后和后尖之前各有一浅而开放的谷；由于原尖的膨大，舌侧的内谷位置非常靠后。

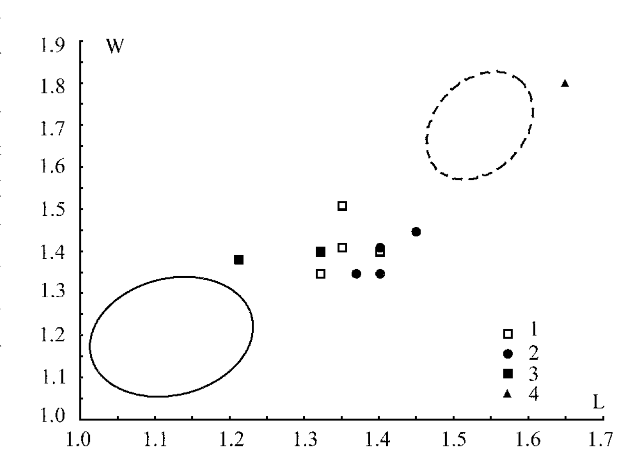


图 4　原跳鼠属各种和副跳鼠属部分种类的 M3 的大小比较

Fig. 4　Comparison of all species of the genus *Protalactaga* and some species of the genus *Paralactaga* in size of M3 Real line–*Protalactaga grabaui* (Quantougou); Broken line–*Paralactaga suni* (Ertemte); 1. *Protalactaga major* (Quantougou); 2. *Protalactaga lantianensis* (Lantian); 3. *Protalactaga moghrebiensis* (Patanik 6, Maroc); 4. *Paralactaga* sp. (Lantian)

比较与讨论　蓝田的这枚 M3 尺寸明显比所有 *Protalactaga* 的种都要大(图 4)，而且齿冠高，冠面构造也简单，这些都表明它不太可能属于 *Protalactaga*。就其大小形态而言，它与 *Paralactaga* 的十分接近，其测量值及简单的构造形式与 *P. suni* 的更为相似，稍有不同的只是外形不太横宽，前边脊相对前尖较发达，中间的凹不太开阔，这些差异在副跳鼠类中可能代表较原始的特征。如果鉴定无误，蓝田的这枚 M3 代表了该属的最早记录。

心颅跳鼠亚科 Cardiocraniinae Vinogradov, 1925

三趾心颅跳鼠属 *Salpingotus* Vinogradov, 1922

原始三趾心颅跳鼠(新种) *Salpingotus primitivus* sp. nov.

(图 3.2, 5.2)

2002 Dipodidae gen. et sp. nov., 张兆群等, p. 170, table 1, 部分标本

2003 Dipodidae gen. et sp. nov., Qiu et al., p. 445, table 1, 部分标本

名称来源　拉丁词 primitivus，表原始之意。

正型标本　1 左 m1(1.00 mm × 0.75 mm)，IVPP V 14438。

模式产地　陕西蓝田第 19 地点。

种征　个体小，齿脊相对齿尖弱，下外脊不明显拉长。

描述　中度磨蚀，属成年个体。牙齿前窄后宽，前内侧显著凹入。齿尖比齿脊相对显著，无下前边尖、下中尖和下中脊。下后尖和下原尖几乎等大，两尖前缘大致处于同一水平，其间齿谷纵向。下内尖横向，比下次尖显著靠前。下次尖膨大且向唇侧凸出。下外脊纵向，下外谷开阔。下次小尖较明显，其位置比下次尖靠后，与下次尖之间有一浅谷，下后边脊不太明显。下内谷较下后边谷浅，但均横向。牙齿后缘轻微向前凹入。

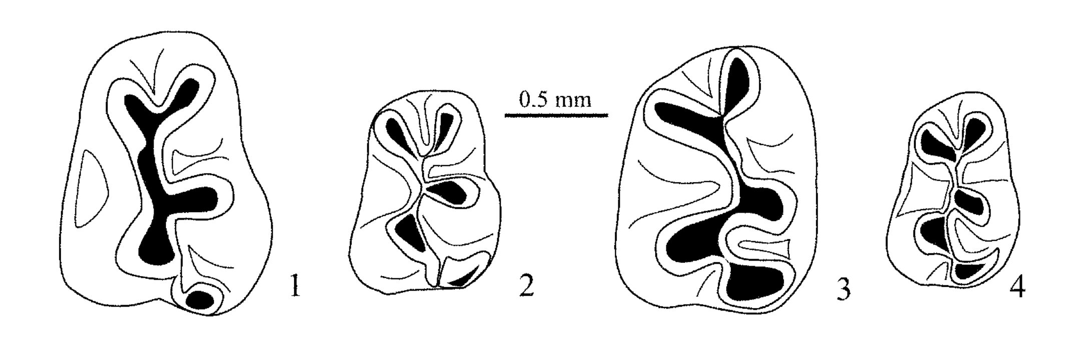


图5 原始三趾心颅跳鼠(新种)、小五趾心颅跳鼠(新种)和现生心颅跳鼠部分属种的m1形态比较

Fig. 5 Comparison of *Salpingotus primitivus* sp. nov. (2), *Cardiocranius pusillus* sp. nov. (4), extant *Salpingotus kozlovi* (1) and *Cardiocranius paradoxus* (3) in morph of m1

1. lm1 (IZ 21274); 2. lm1 (V 14438); 3. lm1 (IZ 25153); 4. rm1 (V 14439, inverse)

比较与讨论 这枚m1以其极小的个体和类似*Dipus*的简单形态构造与心颅跳鼠亚科(Cardiocraniinae)的特征一致。心颅跳鼠亚科是一类侏儒型跳鼠,仅有五趾心颅跳鼠*Cardiocranius* Satunin, 1903和三趾心颅跳鼠*Salpingotus* Vinogradov, 1922两现生属。前者仅有分布于我国西北地区的*C. paradoxus* Satunin, 1903, 为单型属(马勇等,1987);后者在我国记载的有3种:*S. kozlovi* Vinogradov, 1922、*S. crassicauda* Vinogradov, 1928和*S. thomasi* Vinogradov, 1928(王应祥,2003)。对现生两属心颅跳鼠m1的观察发现(见图5),两者在形态上的差异是:*Salpingotus*的狭长、下后尖和下原尖相向排列、下外脊明显拉长;而*Cardiocranius*的则略显短宽、下后尖比下原尖相对明显靠前、下外脊不明显拉长,下次小尖相对*Salpingotus*的要发达。与这两属相比,这枚左m1的形态与*Salpingotus*的基本一致,两者的不同之处仅在于化石的齿脊相对齿尖较弱、下外脊不明显拉长;从图6上可以看到,化石标本明显小于现生*S. kozlovi*。据此,这枚极小的左m1的性状与心颅跳鼠Cardiocraniinae亚科中的三趾心颅跳鼠*Salpingotus*属的较一致。材料虽少,但代表了该属的一个原始种类。以前从未有过

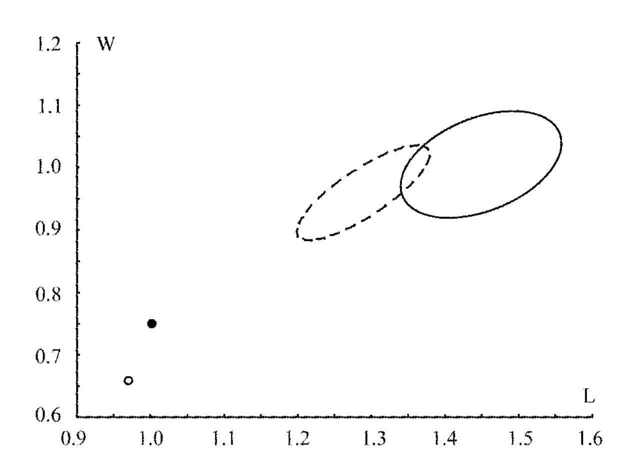


图6 原始三趾心颅跳鼠(新种)、小五趾心颅跳鼠(新种)和现生心颅跳鼠部分属种的m1大小比较

Fig. 6 Comparison of *Salpingotus primitivus* sp. nov., *Cardiocranius pusillus* sp. nov., extant *Salpingotus kozlovi* and *Cardiocranius paradoxus* in size of m1 Real line–*Salpingotus kozlovi* extant (n = 20); Broken line–*Cardiocranius paradoxus* extant (n = 20); Black dot–*Salpingotus primitivus* sp. nov.; Circle–*Cardiocranius pusillus* sp. nov.

Cardiocraniinae 亚科化石的报道,蓝田的这一枚和下面将描述的另一枚极小的 m1 一起代表了 Cardiocraniinae 亚科的首次化石记录和最早出现。

五趾心颅跳鼠属 *Cardiocranius* Satunin, 1903

小五趾心颅跳鼠(新种) *Cardiocranius pusillus* sp. nov.

(图 3.3, 5.4)

2002 Dipodidae gen. et sp. nov., 张兆群等, p. 170, table 1, 部分标本

2003 Dipodidae gen. et sp. nov., Qiu et al., p. 445, table 1, 部分标本

名称来源　拉丁词 pusillus, 表小之意。

正型标本　1 右 m1(0.97 mm × 0.66 mm), IVPP V 14439。

模式产地　陕西蓝田第 19 地点。

种征　个体小,齿脊相对齿尖弱,前部收缩。

描述　牙冠中度磨蚀,属成年个体。牙齿狭长,前部较收缩,呈前内后外向拉伸。齿尖比齿脊相对显著,无下前边尖、下中尖和下中脊。下后尖和下内尖的位置分别明显比下原尖和下次尖的靠前。下外谷开阔,谷缘发育有微弱的齿带。下次小尖非常发达,近三角形,位置比下次尖明显靠后,与下次尖之间有一深狭的谷,下后边脊明显向前弯曲。

比较与讨论　与心颅跳鼠 Cardiocraniinae 亚科仅有的 *Salpingotus* 和 *Cardiocranius* 两属相比,这枚右 m1 以舌侧尖明显比唇侧尖靠前,以及非常发达的下次小尖不同于 *Salpingotus* 属,而与 *Cardiocranius* 属的特征较相似。它与现生种 *C. paradoxus* 相比,其个体显著小,齿脊相对较弱,m1 的前部显著狭窄。据此,这枚右 m1 应为 *Cardiocranius* 属的一个新种。

3　结论

陕西蓝田灞河组中的跳鼠科化石包括 Allactaginae 亚科的 *Protalactaga lantianensis* sp. nov. 和 *Paralactaga* sp. 及 Cardiocraniinae 亚科的 *Salpingotus primitivus* sp. nov. 和 *Cardiocranius pusillus* sp. nov., 其中后一亚科 2 种化石是我国的首次记录和在地史上的首次出现。*Protalactaga lantianensis* sp. nov. 为原跳鼠属的进步种,代表了一种从 *Protalactaga* 向 *Paralactaga* 演进中的过渡类型。*Paralactaga* sp. 为副跳鼠属的最早记录,代表了一种较为原始的副跳鼠。

仅根据跳鼠科化石目前还难以对地层和动物群的时代作较准确的鉴定,但进步的原跳鼠种和原始的副跳鼠种在蓝田灞河组中的共同出现,表明了灞河组的时代应晚于产较原始原跳鼠种的中中新世甘肃咸水河组和内蒙古通古尔组,而早于产进步的副跳鼠种的晚中新世内蒙古二登图组,这符合灞河组的时代为晚中新世早期的观点(张兆群等, 2002; 邱铸鼎等, 2004a)。

现生跳鼠科尤其是 Cardiocraniinae 亚科成员分布于温带干旱地区,适应各种类型的荒漠和半荒漠环境,通常与沙鼠科共同组成荒漠啮齿动物群(马勇等, 1987; 周立志等, 2002)。蓝田灞河组中跳鼠与沙鼠、鼠兔共生(张兆群等, 2002; 邱铸鼎等, 2004b),表明蓝

田地区在晚中新世早期时可能与现今的内蒙古西部荒漠地区相似,气候环境无疑比现在干旱。

致谢 笔者对所有参加中芬合作项目蓝田野外工作的同事们表示衷心的感谢。中国科学院动物研究所马勇、冯祚建教授在我们观察现生标本时给予极大帮助,古脊椎所吴文裕、王伴月研究员热心提供参考资料,王晓鸣博士修改英文摘要,张文定先生拍摄电镜照片,在此一并表示诚挚的谢意。

NOTE ON FOUR SPECIES OF DIPODIDS (DIPODIDAE, RODENTIA) FROM THE LATE MIOCENE BAHE FORMATION, LANTIAN, SHAANXI

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Key words Lantian, Shaanxi, late Miocene, Bahe Formation, Dipodidae

Summary

Although discussion on the phylogenetic classification of jumping mice, birch mice and jerboas is still ongoing, we follow the opinion that the two families Zapodidae and Dipodidae are included in the superfamily Dipodoidea and four subfamilies in the family Dipodidae (Qiu, 1996; Daxner-Höck, 1999), i. e. Allactaginae Vinogradov, 1925, Dipodinae Fischer de Waldheim, 1817, Cardiocraniinae Vinogradov, 1925 and Euchoreutinae Lyon, 1901. The oldest record of Dipodidae is the genus *Protalactaga* from the middle Miocene of Quantougou, Gansu and Tunggur, Nei Mongol, which might be derived from a *Plesiosminthus*-like Oligocene Zapodidae ancestor (Young, 1927; Qiu, 1996, 2000). At the present, Dipodidae are restricted in the Palearctic Region. They are adapted to an arid environment and distributed in semi-desert or desert regions of northern Africa, southern Europe, central and northern Asia. In China, there are 7 genera and 13 species mainly living in the arid northwestern regions (Wang, 2003).

The dipodids described below were collected by the scientists of the Sino-Finish cooperative project in vertebrate paleontology and stratigraphy from Lantian, Shaanxi, during the field seasons of 1997 ~2000.

Protalactaga Young, 1927

Protalactaga lantianensis sp. nov.

(Fig. 1)

Etymology Named after the Lantian area, from where the new species was collected.

Holotype A left M1; IVPP V 14435.

Type locality Loc. 12, Lantian County, Shaanxi Province (China).

Stratum typicum Bahe Formation, early Baodean, early late Miocene.

Paratypes Loc. 12: 44 isolated teeth (5P4, 6M1, 8M2, 4M3, 7m1, 9m2, 5m3), IVPP V 14436.1 ~44; Loc. 19: 2 M2, V 14436.45 ~46; Loc. 6: anterior part of a damaged m2, V 14436.47; Loc. Ms 14: 1m2, V 14436.48.

Diagnosis Large-sized *Protalactaga* with bunodont-lophodont teeth. On M1 ~2 protoloph posteriorly-directed and close to mesoloph; metaloph remarkably postero-situated; posteroloph short and posterolingually-directed. On m1 ~2 hypolophid anteriorly-directed and close to

mesolophid; M3 and m3 relatively more simplified and reduced.

Remarks The specimens are referred to *Protalactaga* due to possession of the following characters: small size; the brachyodont and bunolophodont cheek teeth; the weak anteroloph and anterocone, and the separate protoloph from the mesoloph on M1 ~ 2; the separate mesolophid from the hypolophid on m1 ~2; the strong ectomesolophid of m1.

Three species of *Protalactaga* have so far been recognized. They are *P. grabaui* and *P. major* of middle Miocene from Gansu and Nei Mongol of China, and *P. moghrebiensis* (Jaeger, 1977) of middle Miocene from Jebilet of Morocco.

Protalactaga lantianensis sp. nov. can be distinguished from the three known species in the protoloph and metaloph posteriorly directed on M1 ~2, the hypolophid anteriorly directed on m1 ~2. In addition, the new species differs from *P. grabaui* in its distinctly larger size, the unisolated main cusp on P4 and the stronger lophs, the reduction or absence of mesoloph(id) on M3 and m3. Compared with *P. major*, it has more robust and rounder cusps on cheek teeth, weaker mesoloph(id) on M3 and m3 than *P. major*. Its cusps and lophs are stronger than those of *P. moghrebiensis*.

In *P. grabaui*, the protoloph on M1 transversely connects to the endoloph, while on M2 transversely connects to the protocone; on M1 of *P. major* and *P. moghrebiensis*, it slightly posterolingually connects to the endoloph, while on M2 transversely connects to the endoloph; however, on M1 of *P. lantianensis*, it distinctly posterolingually connects to the endoloph or the base of mesoloph; while on M2 connects to the base or middle of the mesoloph. The metalophs on M1 ~2 of all known species transversely connect to the hypocones or slightly posterolingually connect to the hypoconules; while in *P. lantianensis* they distinctly posterolingually connect to the hypoconules or posterolophs. The hypolophids on m1 ~2 of the three known species do not directly connect to the mesolophids, while in *P. lantianensis* they directly anterolabially connect to the base of the mesolophids. The directions of the protolophs and metalophs on M1 ~2 and the hypolophids on m1 ~ 2 of *P. lantianensis* are similar to those of *Paralactaga*, but the protolophs and metalophs on M1 ~ 2 of *Paralactaga* posteriorly connect to the middle of mesolophs and posterolophs, respectively; the hypolophids on m1 ~2 anteriorly connect to the middle of the mesolophids. In some teeth, the mesoloph on M3 and mesolophid on m3 are absent, consequently the number of the sinuses of these teeth decrease, which differ from those of *P. grabaui* and *P. major*, but are similar to *P. moghrebiensis* and *Paralactaga*. The features similar to *Paralactaga*, namely the distinctly posteriorly oriented protolophs and metalophs on M1 ~2, the anteriorly oriented hypolophids on m1 ~2, the reduction of the third molars, are interpreted as derived characters in *Protalactaga*. It is likely that *P. lantianensis* represents a progressive species of *Protalactaga* at the intermediate stage between *Protalactaga* and *Paralactaga*.

"*Paralactaga minor*" from Loc. 80007 of Tianzhu, Gansu (Zheng, 1982) is similar to *P. lantianensis* in size and morphology. A minor difference includes the direct connection of the hypolophid to the middle part of mesolophid in the m2 of "*P. minor*". The smaller size, lower crown and less robust cusps and lophs seem to group "*P. minor*" into the genus *Protalactaga*.

Paralactaga Young, 1927

Paralactaga sp.

(Fig. 3.1)

Material A left M3, IVPP V 14437.

Locality Loc. Ms 36, Lantian County, Shaanxi Province (China).

Remarks The M3 is larger than that of all known species of *Protalactaga* in size (Fig. 4) and lacks a mesoloph. Accordingly, we refer it to *Paralactaga* rather than *Protalactaga*. Differences of the M3 from that of other known species of *Paralactaga* include the narrower than

length proportions, the distinctly developed anteroloph relative to the paracone, and the narrower sinus. The morphology shown in the M3 is considered primitive characters of the genus *Paralactaga*. If our determination is correct, this single M3 represents the earliest appearance of *Paralactaga*.

Salpingotus Vinogradov, 1922
Salpingotus primitivus sp. nov.
(Fig.3.2, 5.2)

Etymology Primitivus (Latin) means original.

Holotype A left m1; IVPP V 14438.

Type locality Loc. 19, Lantian County, Shaanxi Province (China).

Stratum typicum Bahe Formation, early Baodean, early late Miocene.

Diagnosis Small-sized *Salpingotus* with weaker lophs related to cusps, and relatively short ectolophid on m1.

Remarks This m1 falls into that of Cardiocraniinae in size and structure: tiny size and *Dipus*-like pattern of molar. As a kind of dwarf jerboa, Cardiocraniinae includes so far only two extant genera *Cardiocranius* Satunin, 1903 and *Salpingotus* Vinogradov, 1922. Review of the extant specimens of Cardiocraniinae shows that m1 of *Salpingotus* differs from that of *Cardiocranius* in its longer and narrower outline with less anteriorly situated metaconid relative to protoconid, and the remarkably elongated ectolophid (see Fig. 5). The morphology of this m1 is more similar to that of *Salpingotus* than *Cardiocranius*. Differences of the m1 from that of the extant *S. kozlovi* are the weaker cusps and lophs and narrower posterosinusid. Fig. 6 shows that the fossil tooth is definitely smaller than that of *S. kozlovi*. In view of its extremely small size and highly resemblance to that of *S. kozlovi*, the tooth is treated as a new species of the genus *Salpingotus*.

Cardiocranius Satunin, 1903
Cardiocranius pusillus sp. nov.
(Fig.3.3, 5.4)

Etymology Pusillus (Latin) means tiny.

Holotype A right m1; IVPP V 14439.

Type locality Loc. 19, Lantian County, Shaanxi Province (China).

Stratum typicum Bahe Formation, early Baodean, early late Miocene.

Diagnosis Small-sized *Cardiocranius* with weaker lophs related to cusps, and remarkable narrower anterior portion on m1.

Remarks Compared with the only two genera of Cardiocraniinae, this right m1 differs from that of *Salpingotus* in having a distinctly anteriorly situated metaconid relative to the protoconid, and a more developed hypoconulid. In morphology, it is rather closely similar to the m1 of the extant *Cardiocranius paradoxus*, but differs from the latter in its weaker cusps and lophs, and narrower anterior portion of the tooth. In view of its extremely small size (Fig. 6) and resemblance to that of *C. paradoxus* (Fig. 5), it is considered to be a new species which is referred to the genus *Cardiocranius*.

Conclusions The dipodids from the Lantian assemblage include four taxa *Protalactaga lantianensis* sp. nov., *Paralactaga* sp., *Salpingotus primitivus* sp. nov., and *Cardiocranius pusillus* sp. nov. The former two belong to the subfamily Allactaginae, while the latter two are attributed to the subfamily Cardiocraniinae. *Salpingotus primitivus* sp. nov., and *Cardiocranius pusillus* sp. nov. are the first known fossil records of the subfamily. *P. lantianensis* is the most advanced species of the genus *Protalactaga*, representing an intermediate form between *Protalactaga* and *Paralactaga*. *Paralactaga* sp. might be a primitive species of this genus.

It is difficult to assess a more precise age of Bahe Formation using the dipodids, because of the inadequate knowledge of biochronology for these animals. The presence of *Protalactaga lantianensis*, however, suggests that Bahe Formation is later than the later Middle Miocene, because the Lantian sample seems to be the youngest for its advanced dental characters, while the three known species of the genus *Protalactaga* are of Middle Miocene age. An earlier Late Miocene age is also suggested by the presence of *Paralactaga* sp., which is close to *P. suni* from the later Late Miocene Ertemte, Nei Mongol.

Allactagines and cardiocraniines are widely distributed in temperate arid area and adapted to the desert and semi-desert environments. Generally, they form a typical desert rodent fauna together with gerbils (Ma et al., 1987; Zhou et al., 2002). The concurrence of dipodids, glirids and ochotonids (Zhang et al., 2002; Qiu et al., 2004b) from Bahe Formation might reflect a very arid environment, which may be similar to the desert in western Nei Mongol. It seems that the environment in the Lantian area is dryer during the earlier Late Miocene than the present day.

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